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LONGEVITY, OR LIFE HISTORIES, OF LEAFHOPPER SPECIES ON VIRUS-INFECTED AND ON HEALTHY PLANTS[1]

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INTRODUCTION

IN DISCUSSING the effect of the virus on the insect vector, Leach (1940)[3] has suggested that the question of whether a virus-infected plant is a more favorable host plant than a healthy plant, has been given little attention in virus studies.

Carter (1939), working with yellow-spot of pineapple, found that infected weeds of *Emilia sonchifolia* DC maintain, on an average, higher populations of onion thrips, *Thrips tabaci* Lind., than do healthy plants. He concluded that diseased plants may persist for a longer time, with a mass of curled leaves affording satisfactory shelter for the vector, than do healthy plants which grow rapidly, mature, and die.

It is a well-known fact among entomologists who have carried on field investigations with the beet leafhopper, *Eutettix tenellus* (Baker), that when sugar beets are harvested, the adults fly to other food plants, and a high mortality occurs with the change in host plants. During the 1925 outbreak of the pest, and after the beet tops became dry, enormous numbers of leafhoppers were found in bean fields (Severin and Henderson, 1928), and dead adults were commonly found with their mouth parts inserted in the bean leaves. Tomato plants are favorable host plants of the curly-top virus, but are unfavorable food plants of the beet leafhopper. The decrease in longevity of the males and females on tomato plants has been discussed in a previous paper (Severin, 1928).

During the past seventeen years, 9 leafhopper species have been reported by the author (Severin, 1929, 1934, 1945) to be capable of transmitting the California aster-yellows virus. During the course of an investigation on the longevity of noninfective short-winged *Macrosteles divisus* (Uhler) and long-winged aster leafhoppers—a biological race of the same species (Severin,

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[3] See "Literature Cited" at the end of the paper for complete citations, referred to in the text by author and date of publication.

1940) which had completed their nymphal stages on mildew-resistant Sacramento barley nonsusceptible to the California aster yellows—it was found that low populations of adults of the short-winged leafhoppers were reared, whereas, the long-winged died on healthy celery after the first molt. It was also demonstrated that when both vectors were allowed to reproduce on celery infected with the virus, high populations of adult short-winged aster leafhoppers and low populations of adult long-winged forms were obtained.

Among a large number of newly discovered leafhopper vectors, some species reproduced on both healthy and infected celery; other species multiplied on diseased celery and asters only, and died when transferred to healthy celery and asters; and still other species lived long enough to complete the latent period of the virus but failed to reproduce, and also died when transferred to healthy celery or asters.

Kunkel (1926) found that the latent period of the New York aster-yellows virus in the short-winged aster leafhoppers, using 30 to 100 nymphs or adults in many tests, varied between 10 to 19 days at 70° F. Kunkel (1932) also reported that the latent period of the California aster-yellows virus in the short-winged aster leafhopper, using 30 to 125 nymphs, varied from 19 to 26 days, with an average of 23 days. The latent period of the virus in *Texananus lathropi* Baker varied from 7 to 33 days, in *T. latipex* DeLong from 8 to 37 days, and in *T. spatulatus* Van Duzee from 6 to 35 days, as determined by Severin (1945). Any species of leafhopper which failed to survive on diseased celery or asters for at least 1 week could not be tested as a possible vector, since the latent period of the virus was not completed in the insects.

The present paper deals with the longevity of 9 species of leafhoppers on virus-infected and healthy plants, 5 of which have been previously reported as vectors of the virus (Severin, 1929, 1934, 1945). Another aspect of the problem was to compare the total duration of the nymphal stages of 2 species of phlepsid leafhoppers on healthy and diseased celery plants, and of the beet leafhopper on healthy and curly-top sugar beets.

METHODS

The production of noninfective short-winged and long-winged aster leafhoppers has been described in previous papers (Severin 1929, 1942). The method of obtaining noninfective *Texananus lathropi, T. latipex,* and *Cloanthanus irroratus* (Van Duzee) was similar to that reported for the beet leafhopper (Severin, 1921). The technique used in obtaining noninfective populations of *T. spatulatus* (Van Duzee) has been described in a previous paper (Severin, 1945). In determining the longevity of species of leafhoppers, recently molted adults were used, reared from high populations of last instar nymphs.

LONGEVITY OF SPECIES OF LEAFHOPPERS ON VIRUS-INFECTED AND ON HEALTHY PLANTS

TEXANANUS DENTICULUS OSBORN AND LATHROP

This leafhopper (plate 1, *G, H*) completed the nymphal stages on infected celery, but died on healthy, control celery plants. Fifty males and 50 females were kept singly, each on a healthy celery plant, and a daily record was taken of the mortality of the adults. The longevity of the males ranged from 2 to 20 days, with an average of only 6.9 days; females, from 2 to 33 days, with an average of only 8.4 days.

TEXANANUS PERGRADUS DELONG

This leafhopper vector (Severin, 1945) completed the nymphal stages on experimentally and naturally infected celery, but when transferred to healthy celery the adults died. In testing the efficiency of this vector in transmitting the virus, 50 males and 50 females were kept singly, each on a healthy celery plant during adult life. The longevity of the males ranged from 3 to 8 days, with an average of only 4.8 days; females, from 2 to 12 days, with an average of only 6.7 days.

In another test, 2 lots of 10 recently molted, infective males and females were kept singly, each on a healthy celery plant, and the same number of adults were kept singly on diseased celery plants. On healthy celery, the longevity of 10 males ranged from 3 to 9 days, with an average of only 6.1 days; females, 3 to 22 days, with an average of only 11.6 days.

On infected celery, 10 males and 10 females were alive at the end of 24 days; then equal numbers of males and females were combined on experimentally and naturally infected celery and high populations of adults were reared on both.

TEXANANUS SPATULATUS VAN DUZEE

A comparison was made of the longevity of each leafhopper which transmitted the virus to celery (Severin, 1945) with each adult which failed and, hence, was feeding continuously on healthy celery. The longevity of 34 males which induced the disease ranged from 4 to 144 days, with an average of 45.6 days; and of the 29 females which caused infections, 4 to 198 days, with an average of 51.3 days. The average adult life of 66 males which failed to transmit the virus was 17.9 days; and of 71 females, 20.3 days. Evidently a virus-infected plant prolonged the life of this leafhopper even before symptoms of the disease developed.

This leafhopper completed the nymphal stages on diseased asters. Each of 50 recently molted males and 50 females, which completed the nymphal stages on infected asters, was transferred to a healthy aster, and a daily record of the mortality was taken. The males lived from 1 to 23 days, with an average of only 3.1 days; females, 1 to 28 days, with an average of only 6.3 days. The life cycle was not completed on healthy asters.

CLOANTHANUS IRRORATUS (VAN DUZEE)

The life cycle of this leafhopper was completed on diseased asters. The longevity of 50 males, kept singly, each on a healthy aster, ranged from 1 to 11

days, with an average of only 4.1 days; and of 50 females from 2 to 25 days, with an average of only 10.2 days. The leafhoppers did not complete their life history on healthy asters.

EUSCELES MACULIPENIS DeLONG

The nymphal stages of this leafhopper were completed on diseased asters. The longevity of 50 males on healthy asters ranged from 1 to 35 days, with an average of only 3.4 days; 50 females, 1 to 24 days, with an average of only 3.5 days. This leafhopper also failed to complete the life cycle on healthy asters.

GEMINATE LEAFHOPPER, COLLADONUS GEMINATUS (VAN DUZEE)

As reported in a previous paper (Severin, 1934), the geminate leafhopper was collected on large asters under natural conditions, but a high mortality occurred on small asters in the greenhouse. It was found that adults which were fed on small healthy asters died within a week. The longevity of the last surviving adult of 11 lots of 50 recently molted adults on large healthy asters, ranged from 26 to 123 days, with an average of 84.5 days. Sometimes nymphs completed the nymphal stages when fed on large healthy asters. Nymphs reached the adult stage on diseased asters.

MOUNTAIN LEAFHOPPER, COLLADONUS MONTANUS (VAN DUZEE)

The nymphal stages of the mountain leafhopper were completed on infected asters. The adult life on small asters ranged from 2 to 15 days, with an average of only 4.3 days.

IDIODONUS KIRKALDYI (BALL)

There are numerous leafhopper species which live on diseased celery and asters, but when transferred to healthy plants they die. One illustration will suffice. No attempt has been made to rear *Idiodonus kirkaldyi* on coast sagebrush, *Artemesia californica,* its natural host plant. One lot of 4 adults was kept on infected celery for 66 days, whereas the longevity of 10 males on healthy celery ranged from 1 to 10 days, with an average of only 3.2 days; females, 1 to 6 days, with an average of only 3.4 days. On healthy asters the adult life of the males ranged from 1 to 10 days, with an average of only 8.6 days; females, 1 to 32 days, with an average of only 7.8 days.

COMPARISON OF DURATION OF NYMPHAL STAGES ON HEALTHY AND DISEASED PLANTS

TEXANANUS LATHROPI BAKER

A comparison was made of the interval or period between molts (stages, or stadia—not to be confused with longevity of adults) and the total duration of the nymphal stages of *Texananus lathropi* (plate 1, *A, B, C, D, E, F, I*) reared singly on healthy and diseased celery plants (table 1). In the first experiment, the average total duration of the nymphal stages of the males was 69 days on healthy celery and 51.6, or 7.4 days less, on infected celery; and of the females, 63 days on healthy celery and 60.9, or 2.1 days less, on diseased celery.

In the second experiment, 8 males reared on healthy celery required an average of 51.7 days and 1 male, 52 days on infected celery, or 0.3 days longer on healthy celery.

TABLE 1

DURATION OF STADIA *Texananus lathropi* ON HEALTHY AND ON INFECTED CELERY PLANTS
(Expressed as number of days between molts)

	First instar	Second instar	Third instar	Fourth instar	Fifth instar	Sixth instar	Total
Four males hatched on May 1, and reared on healthy celery plants (first experiment)							
	11	10	9	14	18	..	62
	12	10	9	16	20	..	67
	14	10	10	26	8	..	68
	14	23	13	12	16	1	79
Average	*12.7*	*13.2*	*10.2*	*17.0*	*15.5*	*1*	*69.0*
Five males hatched on May 1, and reared on infected celery plants (first experiment)							
	12	5	9	9	12	..	47
	12	4	8	10	14	..	48
	12	5	8	9	14	..	48
	11	6	7	9	15	..	48
	12	10	9	16	20	..	67
Average	*12.0*	*6.0*	*8.2*	*10.6*	*15.0*	..	*51.6*
Six females hatched on May 1, and reared on healthy celery plants (first experiment)							
	10	7	7	8	16	..	48
	11	8	8	13	16	..	56
	11	8	7	11	20	..	57
	10	7	6	19	21	..	63
	12	11	14	17	17	..	71
	15	23	14	13	18	..	83
Average	*11.5*	*10.7*	*9.3*	*13.5*	*18.0*	..	*63.0*
Seven females hatched on May 1, and reared on infected celery plants (first experiment)							
	13	4	7	4	24	..	52
	12	7	9	10	16	..	54
	12	7	10	9	17	..	55
	15	11	6	16	16	..	64
	13	12	10	10	21	..	66
	14	13	10	10	20	..	67
	15	11	13	10	19	..	68
Average	*13.4*	*9.3*	*9.3*	*9.9*	*19.0*	..	*60.9*
Eight males hatched on August 30, and reared on healthy celery plants (second experiment)							
	12	7	5	8	13	..	45
	10	7	6	9	14	..	46
	11	8	6	8	15	..	48
	12	7	5	8	17	..	49
	11	8	7	9	15	..	50
	11	8	8	10	18	..	55
	12	8	9	8	19	..	56
	12	9	10	11	9	14	65
Average	*11.4*	*7.7*	*7.0*	*8.9*	*15.0*	*14*	*51.7*

TABLE 1 (*Continued*)

	First instar	Second instar	Third instar	Fourth instar	Fifth instar	Sixth instar	Total
One male hatched on August 30, and reared on infected celery plant (second experiment)							
	12	9	7	6	18	..	52
Three females hatched on August 30, and reared on healthy celery plants (third experiment)							
	12	7	5	9	18	..	51
	12	8	7	9	19	..	55
	12	11	11	12	23	..	69
Average	*12.0*	*8.7*	*7.7*	*10.0*	*20.0*	..	*58.3*
Eleven females hatched on August 30, and reared on infected celery plants (third experiment)							
	10	8	6	9	14	..	47
	11	7	6	9	15	..	48
	10	7	6	9	16	..	48
	12	6	5	3	16	..	42
	10	8	6	10	15	..	49
	12	7	8	8	15	..	50
	10	7	7	10	17	..	51
	12	7	8	7	17	..	51
	13	8	7	11	10	5	54
	11	8	6	10	20	..	55
	11	7	6	11	24	..	59
Average	*11.1*	*7.3*	*6.5*	*8.8*	*16.3*	*5*	*50.4*

In the third experiment, the average total duration of the nymphal stages of the females was 58.3 days on healthy celery and 50.4, or 7.9 days less, on diseased celery.

Two nymphs reared on healthy celery passed through six molts; all others, whether on healthy or diseased plants, molted five times.

The life history of *Texananus lathropi* was repeated, but only the total duration of the nymphal stages was determined on healthy and diseased celery plants. The average total duration of the nymphal stages on healthy versus diseased celery plants (table 2) for males was 40.7 days as compared with 38.6 days, and for females, 46.0 days as compared with 40.2 days, demonstrating that the average total duration of the nymphal stages is less on diseased plants.

A statistical analysis of the data on the duration of the nymphal stages of each adult reared on healthy and diseased plants showed no significance.

A high mortality of nymphs occurred when reared on healthy celery plants. A nymphal stage may be greatly prolonged, sometimes a month or longer, but such nymphs die before molting again. Sometimes nymphs die in the process of molting. The mortality of the nymphs was determined with 80 nymphs which hatched on 3 successive days and were placed on 3 healthy celery plants. The nymphs were counted 38 days after hatching and 56 were alive. Forty-four, or 55.0 per cent, of the nymphs reached the adult stage.

A comparison was made of the number of adults reared on healthy and infected celery plants. After their last molt, 10 males and 10 females were confined, 1 pair in each cage which contained either a healthy or diseased celery plant. The number of adults reared from each pair was as follows: healthy celery, 51, 63, 64, 113, and 158, or an average of 97; infected celery, 229, 231, 345, 369, and 395, or an average of 341.

TABLE 2

TOTAL DURATION OF NYMPHAL STAGES OF *Texananus lathropi* HATCHED ON APRIL 26, REARED ON HEALTHY AND ON INFECTED CELERY PLANTS

Number of noninfective males reared	Total duration of nymphal stages of males, days	Number of noninfective females reared	Total duration of nymphal stages of females, days
Reared on healthy celery plants			
1	34	0	..
0	..	1	35
2	39	1	39
2	40	1	40
3	41	0	..
1	42	0	..
0	..	1	43
1	44	2	44
2	45	0	..
0	..	2	46
0	..	1	47
0	..	1	49
0	..	2	50
0	..	1	52
0	..	1	55
0	..	1	56
0	..	1	62
Total 12	*Average 40.7*	*Total 16*	*Average 46.0*
Reared on infected celery plants			
2	34	2	34
0	..	2	36
1	38	1	38
1	39	3	39
1	40	0	..
0	..	1	41
1	42	1	42
0	..	3	45
0	..	2	47
Total 6	*Average 38.6*	*Total 15*	*Average 40.2*

TEXANANUS SPATULATUS VAN DUZEE

A comparison was made of the duration of periods between molts of *Texananus spatulatus* reared on healthy celery with those of leafhoppers on celery infected with aster yellows; and the same comparison was made with rearing on healthy sugar beets and on curly-top beets (table 3), although this leafhopper is not a vector of the curly-top virus.

The average total duration of the nymphal stages of the males was 112

TABLE 3

DURATION OF STADIA OF *Texananus spatulatus* REARED ON CELERY INFECTED WITH ASTER YELLOWS, ON SUGAR BEETS INFECTED WITH CURLY TOP, AND ON HEALTHY PLANTS

Date hatched	Duration of stadia, days						
	First instar	Second instar	Third instar	Fourth instar	Fifth instar	Sixth instar	Total
Males reared on healthy celery plants							
September 30	12	7	5	9	19	..	52
September 25	10	10	14	19	33	..	86
September 25	10	10	8	45	14	..	87
September 24	10	11	8	43	16	..	88
September 24	10	11	10	58	33	..	112
September 2	11	7	6	11	62	18	115
August 30	30	13	9	59	21	..	132
Average	*13.3*	*9.9*	*8.6*	*34.7*	*26.9*	*18.0*	*112*
Males reared on infected celery plants							
September 25	6	14	9	38	17	..	84
September 25	10	10	17	53	21	..	111
September 24	9	12	11	55	26	..	113
Average	*8.3*	*12.0*	*12.3*	*48.7*	*21.3*	..	*102.7*
Females reared on healthy celery plants							
September 25	10	10	11	55	16	..	102
September 25	12	9	29	44	18	..	112
Average	*11.0*	*9.5*	*20.0*	*49.5*	*17.0*	..	*107*
Females reared on infected celery plants							
September 25	9	11	10	46	17	..	93
September 24	11	11	15	49	14	..	100
September 26	11	11	11	42	30	..	105
September 28	6	11	14	65	18	..	114
September 26	11	10	14	61	19	..	115
Average	*9.6*	*10.8*	*12.8*	*52.6*	*19.6*	..	*105.4*
Male reared on healthy sugar beet							
September 25	9	12	12	59	19	..	111
Males reared on infected sugar beets							
September 25	9	11	9	47	15	..	91
September 25	9	11	11	48	17	..	96
Average	*9.0*	*11.0*	*10.0*	*47.5*	*16.0*	..	*93.5*

TABLE 3 (*Continued*)

Date hatched	Duration of stadia, days						
	First instar	Second instar	Third instar	Fourth instar	Fifth instar	Sixth instar	Total
Female reared on healthy sugar beet							
September 25	9	10	13	52	8	19	111
Females reared on infected sugar beets							
September 25	9	11	10	38	17	..	85
September 25	9	11	11	40	15	..	86
September 25	9	11	11	47	17	..	95
September 25	9	11	14	62	16	..	112
Average	*9.0*	*11.0*	*11.5*	*45.4*	*16.2*	..	*94.5*

days on healthy celery and 102.7, or 9.3 days less, on infected celery; and of the females, 107 days on healthy celery and 105.4, or 1.6 days less, on diseased celery.

The total duration of the nymphal stages on healthy versus curly-top beets (table 3) for 1 male was 111 days as compared with an average of 93.5 days for 2 males, and for 1 female, 111 days, compared with an average of 94.5 days for 4 females. These results demonstrate that the average total duration of the nymphal stages is less on diseased plants, even though only 8 adults were reared.

Two nymphs passed through six molts, all others through five.

A statistical analysis of the data on the duration of the nymphal stages of each adult reared on healthy and diseased plants showed no significance.

BEET LEAFHOPPER, EUTETTIX TENELLUS (BAKER)

A comparison was made of the total duration of the nymphal stages of the beet leafhopper, *Eutettix tenellus,* reared on healthy and on curly-top sugar beets (table 4). In three experiments the males required 4.4, 10.3, and 1 days longer on curly-top than on healthy beets; and the females, 1.1, 1.6, and 10.2 days longer. There was no evidence to show that the total duration of the nymphal stages is shorter on curly-top beets than on healthy ones.

SUMMARY

Evidence is presented in this paper that 9 species of leafhopper vectors tested completed the nymphal stages on celery or asters infected with the California aster-yellows virus, but that the adults died when transferred to healthy celery or to asters. The longevity of single males and females of *Texananus spatulatus* was longer on infected celery before symptoms developed than on healthy celery.

The average total duration of the nymphal stages of *Texananus lathropi* was less on infected than on healthy celery, with one exception: where small num-

TABLE 4

TOTAL DURATION OF NYMPHAL STAGES OF *Eutettix tenellus* REARED ON HEALTHY AND ON CURLY-TOP SUGAR BEETS

Number of males reared	Total duration of nymphal stages of males, days	Number of females reared	Total duration of nymphal stages of females, days
Hatched April 30, and reared on healthy sugar beets (first experiment)			
8	36	6	36
4	37	7	37
2	38	4	38
7	39	6	39
6	40	4	40
3	41	6	41
1	42	3	42
1	43	2	43
1	44	1	44
0	..	1	45
1	46	0	..
0	..	1	49
0	..	1	51
Total 34	*Average 40.6*	*Total 42*	*Average 42.1*
Hatched April 30, and reared on curly-top sugar beets (first experiment)			
1	37	0	37
0	38	1	38
1	39	0	39
1	40	1	40
2	41	3	41
6	42	6	42
3	43	4	43
1	44	4	44
1	45	1	45
3	48	1	48
2	49	1	49
1	52	0	..
1	54	0	..
0	..	1	52
1	58	0	..
Total 24	*Average 45.0*	*Total 23*	*Average 43.2*
Hatched May 1, and reared on healthy sugar beets (second experiment)			
3	35	2	35
17	36	23	36
1	37	3	37
3	38	1	38
2	39	0	..
0	..	4	40
0	..	2	41
0	..	1	43
Total 26	*Average 37.0*	*Total 36*	*38.6*

TABLE 4 (*Continued*)

Number of males reared	Total duration of nymphal stages of males, days	Number of females reared	Total duration of nymphal stages of females, days
Hatched May 1, and reared on curly-top sugar beets (second experiment)			
2	39	0	..
3	40	3	40
6	41	7	41
14	42	6	42
7	43	16	43
9	44	5	44
4	45	5	45
5	46	3	46
6	47	5	47
2	48	8	48
1	49	0	..
2	51	1	49
1	52	1	..
1	53	0	..
1	69	0	..
Total 64	*Average 47.3*	*Total 60*	*Average 40.2*
Hatched May 3, and reared on healthy sugar beets (third experiment)			
2	38	0	..
2	39	0	..
10	40	5	40
2	41	7	41
5	42	5	42
0	..	3	43
3	44	2	44
2	45	7	45
0	..	2	46
0	..	1	47
0	..	1	48
Total 26	*Average 41.3*	*Total 33*	*Average 33.0*
Hatched May 3, and reared on curly-top sugar beets (third experiment)			
1	35	1	35
1	36	0	..
1	37	0	..
6	38	1	38
1	39	2	39
5	40	4	40
4	41	3	41
5	42	2	42
1	43	1	43
6	44	5	44
3	45	5	45
2	46	3	46
2	48	2	48
2	49	1	49
1	52	1	52
Total 41	*Average 42.3*	*Total 31*	*Average 43.2*

bers of adults were reared, a high mortality of nymphs occurred on healthy celery and more nymphs were reared to the adult stage on diseased than on healthy celery.

The average total duration of the nymphal stages of *Texananus spatulatus* was less on celery infected with the aster-yellows virus than on healthy plants. The time required for the completion of the nymphal stages on curly-top sugar beets was less than on healthy ones, although this leafhopper is not a vector of the curly-top virus.

A statistical analysis of the data on the duration of the nymphal stages of each adult *Texananus lathropi* and *T. spatulatus* showed no significance.

There was no evidence to show that the total duration of the nymphal stages of the beet leafhopper, *Eutettix tenellus,* is shorter on curly-top sugar beets than on healthy plants.

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PLATE


A


B


C


D


E


F


G


H


I

Plate 1.—Color patterns of nymphal instars and adults of *Texananus lathropi* Osborn and Lathrop: *A*, *B*, *C*, *D*, *E*, first to fifth nymphal instars respectively; *G*, male, and *H*, female. *F*, Male, and *I*, female of *T. denticulus* Osborn and Lathrop.

TRANSMISSION OF CALIFORNIA ASTER-YELLOWS VIRUS BY THE FIRST REPORTED LEAFHOPPER VECTOR IN GYPONINAE

HENRY H. P. SEVERIN

TRANSMISSION OF CALIFORNIA ASTER-YELLOWS VIRUS BY THE FIRST REPORTED LEAFHOPPER VECTOR IN GYPONINAE[1]

HENRY H. P. SEVERIN[2]

INTRODUCTION

SEVERIN reported evidence that 10 leafhopper species and a biological race of one species (1940) transmit the California aster-yellows virus (1929, 1934, 1945).[3] The present paper deals with the transmission of the virus by *Gyponana hasta* DeLong. The characters, distribution, and food plants of this leafhopper have been discussed by DeLong and Severin (1946) in a companion paper.

An investigation was undertaken on the transmission of the virus to healthy celery and asters by single males and females and by varying numbers of adults. Experiments were conducted to determine the latent period and the retention of the virus in the adults, and whether this leafhopper could transmit the viruses of curly top and of Pierce's disease of grapevines. Life history studies were undertaken on the egg periods, egg-laying capacity, and duration of the nymphal stages. Measurements of various parts of the body were taken of each nymphal instar and of the adults.

METHODS

To determine the latent period of the virus in the adults, high populations of noninfective leafhoppers were reared on California common, or Chilean alfalfa, *Medicago sativa,* which is nonsusceptible to the disease. Infective leafhoppers were reared on celery infected with the virus. Life history studies were undertaken with nymphs which hatched from eggs deposited in the petioles of diseased celery. After determining the egg periods, the petioles in which oviposition occurred were cut into pieces a day or two before hatching and placed in stender dishes, the bottoms of which were covered with moist filter paper. Each nymph which hatched was transferred to an infected celery plant, and daily observations were made to determine each molt.

TRANSMISSION OF VIRUS TO CELERY

By Single Males and Females.—The efficiency of the vector in the transmission of the virus to healthy celery was determined with 50 males and 50 females. (The nymphal stages on diseased celery required an average of 84.5 and 81.0 days, respectively, during January and February, as shown in table 6.) Each leafhopper was kept on a healthy celery plant until symptoms of the disease developed, or during adult life if no symptoms appeared. Table 1 indicates that 18 per cent of the males and 12 per cent of the females caused infections.

[1] Received for publication November 15, 1945.

[2] Entomologist in the Experiment Station.

[3] See "Literature Cited" for complete citations, referred to in the text by author and date of publication.

TABLE 1

TRANSMISSION OF VIRUS TO SUCCESSIVE SETS OF CELERY, BY VARYING NUMBERS OF *Gyponana hasta*

Number of lots	Number of adults in each lot	First set of celery			Second set of celery			Third set of celery			Fourth set of celery			Total		
		Plants inoculated	Plants infected	Per cent infected	Plants inoculated	Plants infected	Per cent infected	Plants inoculated	Plants infected	Per cent infected	Plants inoculated	Plants infected	Per cent infected	Plants inoculated	Plants infected	Per cent infected
50	1 male	50	9	18.0	..	..	....	..	..	....	..	..	....	50	9	18.0
50	1 female	50	6	12.0	..	..	....	..	..	....	..	..	....	50	6	12.0
25	5 males	25	6	24.0	22	3	13.6	22	2	9.1	..	..	....	69	11	15.9
25	5 females	25	6	24.0	24	2	8.3	23	0	0.0	2	1	50.0	74	9	12.2
25	10 males	25	15	60.0	22	0	0.0	20	0	0.0	7	0	0.0	74	15	20.3
16	10 females	16	5	31.2	15	1	6.7	15	0	0.0	1	0	0.0	47	6	12.8
25	20 males	25	12	48.0	23	6	26.1	22	1	4.5	22	0	0.0	92	19	20.7
17	20 females	17	2	11.8	17	3	17.6	16	1	6.2	16	0	0.0	66	6	9.1

By Varying Numbers of Adults.—An experiment was conducted with lots of 5, 10, and 20 adults which had completed the nymphal stages on diseased celery, to determine the percentages of transmission of the virus. Each lot of adults was kept on a healthy celery plant until symptoms of the disease appeared and then was transferred to a second healthy plant. If no symptoms developed within 30 days, the surviving adults were transferred monthly to successive healthy plants during adult life. The results obtained with the four sets of celery plants are shown in table 1. A comparison of the percentages of infections of the first set of celery plants shows that lots of 5 males and 5 females each infected 24.0 per cent of the celery; lots of 10 males and 10 females, 60.0 and 31.2 per cent, respectively; and lots of 20 males and 20 females, 48.0 and 11.8 per cent, respectively. The total percentages of infections produced by males were somewhat higher than those by females.

TRANSMISSION OF VIRUS TO ASTERS

By Single Males and Females.—The transmission of the virus to healthy asters was determined with 50 males and 50 females which had completed the nymphal stages on diseased celery. Each leafhopper was transferred and kept singly on a healthy aster plant during adult life. Table 2 shows that 1 of 50 females caused an infection and no infections were produced by the males. If this result is compared with the percentage of transmission of the virus to celery under the same conditions, it is evident that celery is more readily infected than asters (table 1).

By Varying Numbers of Adults.—A comparison was made of the infections produced by varing numbers of adults transferred to successive healthy asters every week or every 2 weeks. Each lot of leafhoppers was transferred to from 6 to 12 successive asters until the last adult died. A record was taken of the mortality of the adults. Table 2 records the results with 6 successive sets of asters. No infections were obtained with aster sets 7 to 12; hence, these are not included in the table. Lots of 10 males caused no infections of 30 asters inoculated every week, but 16.7 per cent of the asters were infected which had been inoculated every 2 weeks. In the weekly inoculations of successive asters with lots of 20 males, 6.7 per cent were infected, and 20.0 per cent of the asters were infected which had been inoculated every 2 weeks. Lots of 5 males infected 1.7 per cent of the asters inoculated every 2 weeks. Higher percentages of infections were obtained with lots of 10 and 20 males when asters were inoculated every 2 weeks rather than every week.

TRANSMISSION OF VIRUS TO TWO HOST PLANTS

Inoculations of one set of healthy celery and three successive sets of healthy asters for periods of 3 weeks were made with lots of 20 infective males which had completed the nymphal stages on diseased celery. Mortality records were taken with each transfer of the adults. The results (not tabulated) show that 11 of 21 of the first set of celery and the same number of the first set of asters were infected, or 52.4 per cent each; 6 of 21 asters of the second set were infected, or 28.6 per cent; and 1 of 19 asters of the third set was infected, or 5.3 per cent. The lower percentage of transmission of the virus to the third set of asters can be attributed to the mortality of the males. When these results

TABLE 2

TRANSMISSION OF VIRUS TO SUCCESSIVE SETS OF ASTERS, BY VARYING NUMBERS OF *Gyponana hasta*

Number of lots	Number of adults in each lot	First set of asters		Second set of asters		Third set of asters		Fourth set of asters		Fifth set of asters		Sixth set of asters		Total			Adults alive at end of 6 or 12 weeks
		Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Per cent infected	
50	1 male	50	0	..	..	..	..	..	..	..	..	..	..	50	0	0.0	.....
50	1 female	50	1	..	..	..	..	..	..	..	..	..	..	50	1	2.0	.....
							Weekly inoculations										
5	10 males	5	0	5	0	5	0	5	0	5	0	5	0	30	0	0.0	1 to 5
5	20 males	5	1	5	0	5	1	5	0	5	0	5	0	30	2	6.7	12 to 16
							Inoculations every 2 weeks										
10	5 males	10	0	10	1	10	0	10	0	10	0	10	0	60	1	1.7	1 to 4
5	10 males	5	1	5	1	5	1	5	0	5	1	5	1	30	5	16.7	2 to 7
5	20 males	5	1	5	1	5	1	5	1	5	1	5	1	30	6	20.0	4 to 10

are compared with those obtained in table 2, in exposures of 1 and 2 weeks to the first or second set of asters, and with the same number of leafhoppers, it is evident that larger numbers of infections were obtained when inoculations were made during periods of 3 weeks, again demonstrating that the periods of exposure are a factor in the transmission of the virus.

TABLE 3

LATENT PERIOD OF VIRUS IN FIVE LOTS OF FORTY FEMALE *Gyponana hasta*, WITH CELERY AS THE HOST PLANT

Days on infected celery	Successive plants inoculated	Plants infected	Per cent infected	Days after transfer on which successive infections occurred, including initial day on infected celery	Adults alive at end of 42 days
1	41	2	4.9	19, 40	20
1	41	1	2.4	20	23
1	41	4	9.8	24, 26, 32, 33	18
1	41	4	9.8	33, 35, 38, 39	16
1	41	1	2.4	35	16

TABLE 4

LATENT PERIOD OF VIRUS IN VARYING NUMBERS OF ADULT *Gyponana hasta*

Number of adults	Days on infected celery	Successive plants inoculated	Plants infected	Per cent infected	Days after transfer on which successive infections occurred, including initial 10 to 15 days on infected celery	Adults alive at end of 42 days
20	10	32	2	6.2	26, 38	10
20	10	32	3	9.4	28, 32, 35	6
20	10	32	2	6.2	34, 42	12
10	15	27	1	3.7	13	4
10	15	27	2	7.4	16, 29	2
10	15	27	5	18.5	25, 31, 35, 36, 40	2

LATENT PERIOD OF VIRUS IN ADULTS

The latent period of the virus was determined with 5 lots of 40 females. Each lot of leafhoppers was kept on a diseased celery plant for 1 day and then was transferred daily to successive healthy celery for a period of 41 days. The minimum latent period of the virus ranged from 19 to 35 days, as is shown in table 3.

Lots of 5 and 10 adults kept on infected celery plants for 1 day, and then transferred daily to healthy celery for 41 days caused no infections (not tabulated). It was decided to increase the period of exposure on diseased celery to 10 days, with 3 lots of 20 adults, and 15 days, with 3 lots of 10 adults. The number of infections obtained is indicated in table 4. One lot of 10 males produced 5 infections, compared with 4 infections by each of 2 lots of 40 females, as shown in table 3. The latent period of the virus cannot be determined accurately with exposures of 10 and 15 days on infected celery, since the virus may have been acquired on the first or succeeding days. Each of 2 lots of 20 and 10 adults failed to produce infections and were not tabulated.

RETENTION OF VIRUS BY SINGLE ADULTS

The retention of the virus was determined with single males and females which had completed the nymphal stages on diseased celery. Each leafhopper, after producing the first infection on a healthy celery plant, was transferred daily during adult life to successive healthy plants. The results are shown in table 5. The virus was retained for a period of 11 to 46 days by 2 males. Three males and 2 females produced only the initial infection. The period of the first infection is not included in the retention of the virus, since the adults were able to acquire the virus again.

TABLE 5

RETENTION OF VIRUS BY SINGLE ADULT *Gyponana hasta* WITH CELERY AS THE HOST PLANT

Days on first plant before symptoms developed	Plants inoculated after first infection	Plants infected after first infection	Per cent infected after first infection	Days after first infection on which successive infections occurred	Longevity of adults, days
Five lots of males					
41	12	3	25.0	43, 44, 46	76
55	75	1	1.3	11	131
49	13	0	0.0	0	241
70	23	0	0.0	0	93
119	19	0	0.0	0	127
Two lots of females					
28	28	0	0.0	0	121
36	8	0	0.0	0	150

ATTEMPTS TO TRANSMIT VIRUSES OF CURLY TOP AND PIERCE'S DISEASE OF GRAPEVINES

An attempt was made to transmit the curly-top virus by means of *Gyponana hasta*. One lot of 20 males was transferred daily, alternating with curly-top sugar beets and healthy beets, but no infections were produced. Five lots of 50 males or females were exposed to curly-top beets for 2 days and then were transferred daily to successive healthy beets during adult life. Thirty-two healthy beets were inoculated but no disease resulted. The last adult in each lot survived from 6 to 12 days, an average of 8.8 days on beets.

Eighteen tests were made with lots of 20 adults each to transmit the virus from Pierce's disease of grapevines to 5 healthy grapevines and to 5 healthy California common (Chilean) alfalfa and from alfalfa dwarf to 8 healthy alfalfa plants of the same variety. All inoculated grapevines and alfalfa remained healthy. The virus of Pierce's disease of grapevines is identical with the virus of alfalfa dwarf (Houston, Frazier, and Hewitt, 1945).

LIFE HISTORY

Egg Periods.—The egg periods of *Gyponana hasta* were determined with eggs deposited in the petioles of celery during January. Females at the egg-laying stage were confined in a cage enclosing a large celery plant for 1 day.

Eggs deposited during that day hatched over a period of 4 days; the maximum hatching occurred during the first day. The egg periods required from 22 to 26 days under greenhouse conditions.

Egg-laying Capacity.—To determine the number of eggs which a female

TABLE 6

DURATION OF PERIODS BETWEEN MOLTS IN NYMPHAL STADIA OF *Gyponana hasta*

Date hatched	Duration of stadia, days					
	First instar	Second instar	Third instar	Fourth instar	Fifth instar	Total
Males						
February 2	10	12	13	19	19	73
January 30	8	10	17	17	23	75
January 25	10	14	13	19	20	76
January 24	8	8	19	20	23	78
February 4	10	10	12	28	18	78
January 18	9	10	13	31	18	81
February 2	10	12	13	16	30	81
February 5	9	10	13	25	25	82
February 5	10	13	16	25	21	85
January 30	8	11	14	30	23	86
January 30	10	8	13	40	18	89
January 29	8	11	14	36	25	94
January 20	10	20	19	29	18	96
January 30	10	12	12	75	..	109
Average	*9.3*	*11.6*	*14.4*	*29.3*	*21.6*	*84.5*
Females						
February 2	10	12	13	19	17	71
January 25	10	19	13	16	17	75
January 21	12	11	14	16	23	76
February 2	10	13	13	19	22	77
February 7	8	11	14	25	17	77
February 8	10	13	14	23	18	78
January 30	10	13	12	25	19	79
January 21	9	11	14	29	17	80
January 22	7	7	15	31	20	80
January 30	8	15	20	24	13	80
February 3	9	11	13	27	20	80
February 7	10	15	13	21	22	81
February 2	10	12	13	27	22	84
February 8	10	14	17	21	22	84
January 23	8	8	14	35	22	87
January 22	12	12	11	37	17	89
January 24	9	18	14	22	26	89
January 22	10	15	16	31	19	91
Average	*9.6*	*12.8*	*14.1*	*24.9*	*19.7*	*81.0*

deposits during her adult life, 1 female and 1 male were confined in a cage enclosing a large alfalfa plant. The eggs were allowed to hatch and the total number of nymphs removed from the cage would equal the egg-laying capacity, providing all of the eggs hatched. The nymphs were removed twice during each month from the cage. A total of 361 nymphs hatched.

Duration of Stadia.—The interval, or period, between molts (stages, or stadia) and the total duration of the nymphal stages were determined on diseased celery used as a food plant as indicated in table 6. The males required from 73 to 109 days, with an average of 84.5 days, to complete the nymphal stages; and the females from 71 to 91 days, with an average of 81 days. One nymph, a male, passed through four molts requiring 75 days to complete the fourth stadium, compared with 16 to 40 days, or an average of 25 days with males that passed through five molts. All females passed through five molts.

Measurements of Nymphal Instars and Adults.—Table 7 gives the average measurements of various parts of the body 1 day after hatching and 1 day after each molt of lots of 10 nymphs, 14 males, and 20 females. Using data from table 7, each instar can be determined from the range in measurements:

TABLE 7

AVERAGE MEASUREMENTS IN MILLIMETERS OF INSTARS AND ADULTS OF *Gyponana hasta*

Nymphs and adults	Diameter of head across compound eyes			Length of head, thorax, and abdomen			Length of head to end of wings		
	Maximum	Minimum	Mean	Maximum	Minimum	Mean	Maximum	Minimum	Mean
First instar.....	0.63	0.61	0.62	1.54	1.35	1.44	....	....	....
Second instar...	0.84	0.76	0.79	2.67	2.24	2.39	....	....	....
Third instar....	1.07	1.00	1.03	3.51	3.19	3.31	....	....	....
Fourth instar...	1.43	1.31	1.38	5.05	4.59	4.80	....	....	....
Fifth instar....	1.88	1.67	1.80	6.83	6.02	6.59	....	....	....
Males.....	1.85	1.75	1.80	8.71	6.89	8.12	8.58	6.89	8.16
Females.....	2.15	1.89	2.01	9.58	8.10	8.94	9.55	8.50	9.15

the diameter of the head across the compound eyes, and the length of the head, thorax, and abdomen. Average measurements of the male and female leafhoppers that completed five molts show that the males are smaller than the females. The measurements of the male which molted four times (not tabulated) were as follows: diameter, head across compound eyes, 1.80 mm.; length, head and abdomen, 8.15 mm.; and length, head to end of wings, 8.15 mm. It is evident that the male, which molted four times, was not smaller than the average measurements of the males that passed through five molts.

Color of Nymphal Instars and Adults.—The nymph, upon hatching, is white, but later assumes a yellow tinge with reddish-brown areas on the posterior region of the head, on the pronotum, and on the anterior portion of the abdomen. The second and third nymphal instars are green and the fourth and fifth nymphal instars are pale green. These typical color patterns are shown in plate 1. The male and female are green.

Color variations of all nymphal instars occur, with the exception of the first instar as shown in plate 2.

SUMMARY

Fifty males and 50 females reared on diseased celery and tested singly on healthy celery caused 18 and 12 per cent infections respectively. One of 50 females reared on diseased celery infected 1 aster; no infection was produced by 50 males tested singly on asters.

The infections of successive celery plants in monthly transfers for 4 months by lots of 5 males and 5 females were 15.9 and 12.2 per cent respectively; by lots of 10 males and 10 females, 20.3 and 12.8 per cent respectively; and by lots of 20 males and 20 females, 20.7 and 9.1 per cent respectively.

A comparison of the transmission of the virus to successive asters by varying numbers of adults was as follows: by lots of 20 males in weekly inoculations, 6.7 per cent; inoculations every 2 weeks, 20.0 per cent; by lots of 10 males in weekly inoculations, 0.0 per cent; and for 2 weeks, 16.7 per cent; and by lots of 5 males during 2-week intervals, 1.7 per cent.

During periods of 2 weeks, inoculations of two host plants by lots of 20 males resulted in the following percentages of infections: first set of celery and first set of asters, each 52.4 per cent; second set of asters, 28.6 per cent; and third set of asters, 5.3 per cent. Asters are less readily infected than celery.

The minimum latent period of the virus in the adults ranged from 19 to 35 days.

The virus was retained for a period of 11 to 46 days. Most of the adults produced 1 infection and then apparently lost the infective dose.

Attempts to transmit the viruses of curly top and Pierce's disease of grapevines (alfalfa dwarf) by this leafhopper were failures.

Life history studies were made of the egg periods, egg-laying capacity, and duration of the nymphal stages.

The total duration of the nymphal stages of the males required from 73 to 109 days, with an average of 81 days; females required from 71 to 91 days, with an average of 81 days. One male passed through four molts, all others through five molts. Each instar can be determined accurately from tabulated measurements giving diameter of the head across the compound eyes, and the length of the head, thorax, and abdomen.

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PLATES

Plate 1.—Color patterns of nymphal instars and adults of *Gyponana hasta*: *A*, first nymphal instar, yellow in color with reddish-brown areas on the anterior portion of the abdomen, pronotum, and posterior region of the head; *B*, *C*, second and third nymphal instars, green in color; *D*, *E*, fourth and fifth nymphal instars, pale green; *F*, male and *G*, female, both green in color.

A

B

C

D

E

F

Plate 2.—Color variations of instars of *Gyponana hasta*: *A*, second instar; *B*, *D*, third instars; *C*, *E*, fourth instars; and *F*, fifth instar.

TAXONOMY, DISTRIBUTION, AND FOOD PLANTS OF *GYPONANA HASTA*, A LEAFHOPPER VECTOR OF CALIFORNIA ASTER-YELLOWS VIRUS

DWIGHT M. DeLONG AND HENRY H. P. SEVERIN

TAXONOMY, DISTRIBUTION, AND FOOD PLANTS OF *GYPONANA HASTA*, A LEAFHOPPER VECTOR OF CALIFORNIA ASTER-YELLOWS VIRUS[1]

DWIGHT M. DeLONG[2] AND HENRY H. P. SEVERIN[3]

INTRODUCTION

SEVERIN has previously reported (1934, 1940)[4] that 3 species and a biological race of leafhoppers transmit the California aster-yellows virus. In two recent papers DeLong and Severin (1945) and Severin (1945) added 6 species of phlepsid leafhopper as vectors of this virus. The present paper deals with the characters, distribution, and food plants of one additional leafhopper vector, *Gyponana hasta* DeLong; in a companion paper, Severin (1946) discusses the transmission of the virus by this, the first reported leafhopper vector in the subfamily Gyponinae.

CHARACTERS, DISTRIBUTION, AND FOOD PLANTS

For several years *Gyponana hasta*, recently described (DeLong, 1942), has been confused with and identified as *Gyponana angulata* Spangberg, which it resembles very closely in general appearance and in morphologic structures.

Gyponana hasta is one of the few species of this genus with an angled vertex. This species is similar to *G. angulata* in general appearance, and can be distinguished from it only by the shape of the style and aedeagus. Its length is 7.5 to 9 mm.

The vertex is somewhat strongly produced and bluntly angled, and is two thirds as long at the middle as the basal width between the eyes.

In color it is somewhat variable, but usually is dull yellow with a tinge of green. The vertex, pronotum, and scutellum (plate 1, *A* and *B*) are often definitely yellow. There are no dark nor definite color markings.

The female last ventral segment has a posterior margin which is broadly, concavely excavated, with a slight median notch (plate 1, *C*).

The male plates are elongate, blunt at the apex, and with a slight bulge on the outer margin near the middle (plate 1, *D*). The aedeagus (plate 1, *E*) is long and somewhat slender, with a pair of short terminal, lateral processes which extend about one third of the distance to the basal curved part and are closely appressed to the body of the aedeagus. The style is sickle-shaped, with the apical half broadened at the base, then gradually tapered to a sharp-pointed apex (plate 1, *F*).

In comparison with *Gyponana angulata*, the styles are longer and the tapered part is more slender before the apex. The aedeagus is longer, narrower, with shorter lateral processes which are more closely appressed.

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[3] Entomologist in the Experiment Station.

[4] See "Literature Cited" for complete citations, referred to in the text by author and date of publication.

Geographic Range.—The species was originally described from specimens taken in Arizona in the following localities: Hualpai and Patagonia mountains, Sabino Canyon, Williams, Turkey Creek, and Granite Dells. In California, earlier records indicate that specimens were taken at Sacramento, Mint Canyon, Hamilton City, Mt. Shasta, and Freeport; in Texas, at Fort Davis and in Gillespie and Val Verde counties; in Oregon, at Mt. Hood; in Idaho, at Coeur d'Alene; in Washington, at Mt. Rainier; in Utah, at Snyderville; and in Missouri, at Cabool.

Distribution and Food Plants in California.—The localities and food plants of this leafhopper are as follows:

San Luis Obispo County: 1 pair was collected in a pasture at Santa Maria, June 12, 1942, by N. W. Frazier.

San Diego County: 1 nymph (a male after the last molt) was taken in a field of alfalfa, *Medicago sativa,* at Boulevard, June 7, 1942, by N. W. Frazier.

San Bernardino County: On June 5, 1942, at the entrance to Cajon Pass several adults were captured on squaw bush, *Rhus trilobata* by N. W. Frazier.

Imperial County: At Westmoreland, June 7, 1942, 1 pair was caught in an alfalfa field by N. W. Frazier.

Tulare County: On May 8, 1941, at Woodlake 8 adults were captured in an alfalfa field by N. W. Frazier.

Fresno County: Adults were obtained in sweepings of alfalfa fields in the vicinity of Sanger, Selma, and Biola by H. H. P. Severin, and at Palier on April 15, 1942, by N. W. Frazier.

Madera County: At Madera, October 9, 1941, a few adults were taken in an alfalfa field by H. H. P. Severin.

Merced County: On April 28, 1943, at Livingston, 1 male and 2 females were collected on sagewort, or mugwort, *Artemisia vulgaris,* by N. W. Frazier.

Stanislaus County: On July 2, 1942, 6 males and 4 females were obtained in sweepings of alfalfa fields at Newman by N. W. Frazier.

Napa County: At Dry Creek School, February 13, 1943, a pair was caught in general sweepings, but the host plant was not recorded by N. W. Frazier.

Sacramento County: In a locality known as "Sacramento Pocket," on September 12, 1941, 2 adults were taken in a field of Ladino clover, *Trifolium repens* L. var. *latum* McCarthy, by H. H. P. Severin.

Among economic plants, this leafhopper was collected on one occasion in a celery field near Terminus, in the Sacramento Valley.

The collection data indicate that this leafhopper overwinters in the adult stage.

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PLATE

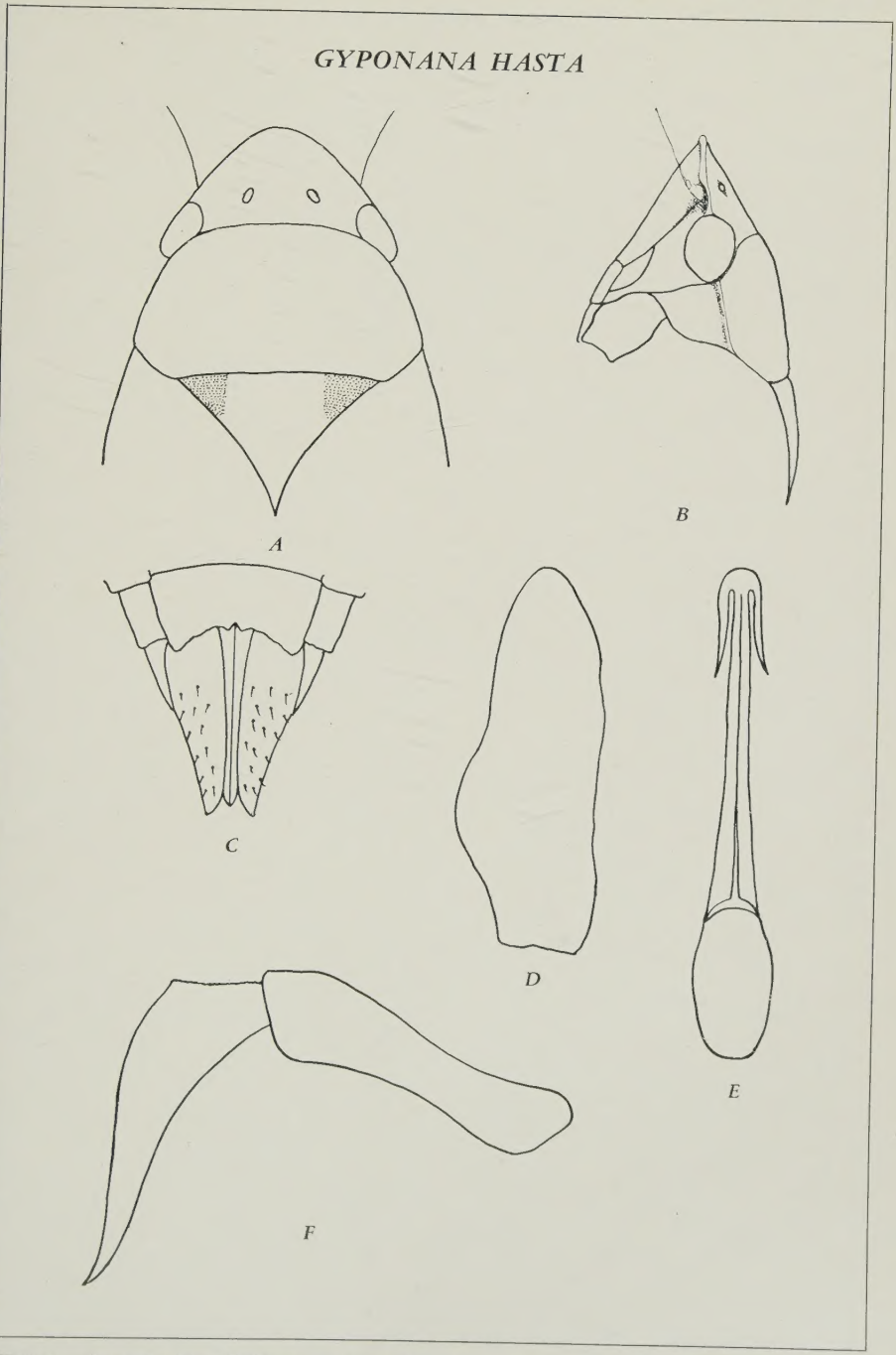

Plate 1.—*Gyponana hasta* DeLong: *A*, dorsal view of head, pronotum, and scutellum; *B*, lateral view of head, pronotum, and scutellum; *C*, ventral view of female external genital structures; *D*, ventral view of male plate; *E*, ventral view of male aedeagus; *F*, lateral view of male style.